4. *A Tabulate Coral from the Bokkeveld Beds of South Africa.*

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(With Text-figure 30.)

In view of the rarity of fossil corals in the Bokkeveld beds of South Africa, special interest attaches to the tabulate coral recently found by the writer at Gamka Poort, particularly on account of the wide distribution of this genus in the Lower Devonian of Europe and America. No tabulate coral has as yet been recorded from the Devonian of South Africa.

Pleurodictyum bokkeveldense sp. nov.

Locality and Stratigraphic Horizon.—The specimen to be described was found at Gamka Poort in the Zwarteberg mountains of the Cape. Its stratigraphic position is near the bottom of the series—that is to say, within the lowest of the five shale horizons of the Bokkeveld, below the first sandstones.

Mode of Occurrence.—Only one specimen was found, and this occurs in the form of a cast in a tough micaceous and arenaceous mudstone.

Description.—Compound, corallum discoidal and rather flat. Outer edge not completely preserved, but outline appears to be slightly oval, almost circular. Upper surface of corallum rather convex. Walls of corallites mostly thick, varying in thickness from ·2 to ·9 mm., with fairly numerous, irregular pores. Septa rudimentary, indicated by nodose and denticulated radial ridges of varying strength. They are weakly defined within the lower interior portion of cells by radial lines of low, inconspicuous, granular spikes, but more strongly developed in upper portion of cells around their edges, where they are represented by fairly consistent and regular nodose ridges.

Since the specimen is preserved as a cast, the visceral cavity of each corallite being filled with mud, no tabulae can be discerned. Several of the marginal corallite-casts, however, exhibit a distinct groove running around their outer marginal side half-way up their

preserved heights. Possibly these features represent rudimentary tabulae, or tabulae in incipient stages of growth.

The individual corallites diverge from the centre of the base and are oriented more or less at right angles to the curved, convex surface

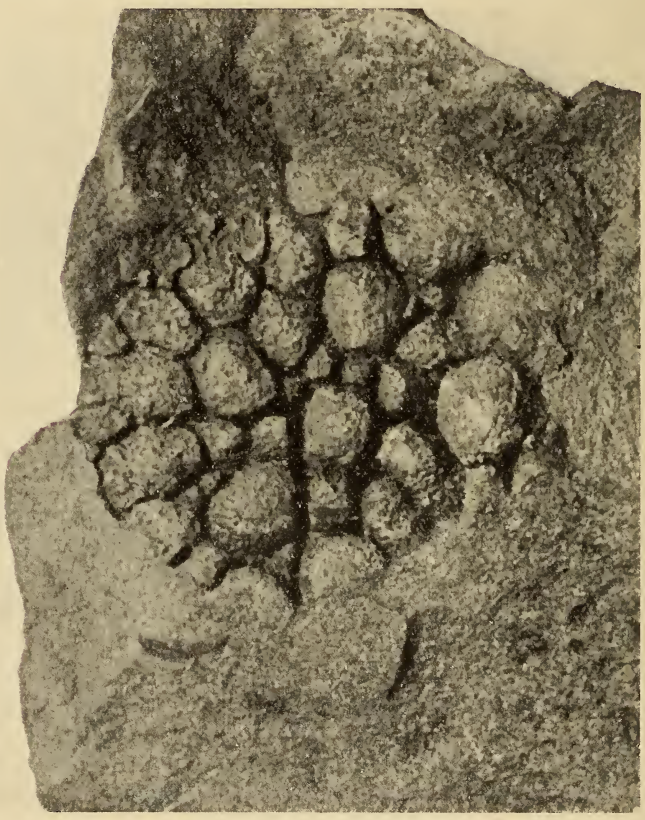

Fig. 30.—*Pleurodictyum bokkeveldense*. × 2½.

of the corallum. All of them taper towards the base, thus having a distinct funnel-shaped appearance. This feature is particularly strongly developed in the smaller and narrower, probably younger, cells that are irregularly situated between wider and deeper ones.

While generally polygonal, their outline varies considerably. None of them are hexagonal in form. The larger and deeper ones, while still polygonal, are almost rounded, circular, and oval in outline. Rectangular shapes are not infrequent in the case of the smaller, narrower cells.

The specimen shows 34 cells in all and, although not completely preserved along part of the margin, the total number of cells probably was not more than about 40 to 43. The great variety in outline of the individual cells has already been mentioned, but a still more characteristic feature is their great divergency in size. While the largest attain a width of 5 to 6 mm., casts of the smallest are represented merely by a long or short tapering spike of 2 to 3 mm. diameter at the base of the cast (surface margin of corallite). Owing to the great divergency in shape and size of the individual cells, a true radial symmetry of the corallum is not at once apparent. If the missing marginal portion of the corallum, however, is reconstructed, it is seen that there is a large central cell round which the others are concentrically grouped. The great divergency of the cells, however, particularly in size, to a large extent obscures this radial symmetry. Sometimes a number of large cells adjoin, and groups of small ones also occur. The latter, however, do not occur as clusters, but where present in greater numbers exhibit a linear arrangement in the intervening space between larger ones. These features distinguish the form under discussion from other known species of the same genus.

Dimensions.—Unfortunately the specimen is not completely preserved in some of the marginal portions of the corallum, but the latter possesses a longest diameter of 2·6 cm. and a shortest diameter of 2·4 cm. approximately.

Affinities.—This form is very different from *Pl. lenticulare* Hall. var. *laurentium* commonly found in the Helderbergian (Lower Devonian) of New Scotland, North America. The latter is characterised by its very large and few cells, the walls of which are strongly marked by nodose and broken septa. There is a central cell, hexagonal in form, bounded by six other similar cells. The lenticular corallum frequently grows to a large size, showing three cycles of hexagonal cells around the central cell.

From this species *Pl. bokkeveldense* differs mainly through the marked irregularity in the size, shape, and arrangement of the individual cells.

A somewhat closer relationship is shown to *Pl. styloporum*, found in the Middle Devonian of North America, the corallum of which, however, is not nearly as discoidal, but attains a considerably greater height.

A still closer relationship is shown to the well-known *Pl. problematicum* Goldf. which is very common in the spirifer-bearing greywackes and sandstones of the Lower Devonian of the Rhineland. This form

possesses a flat, discoidal corallum of circular or oval outline and is also invariably found as a cast. The corallum of *Pl. bokkeveldense*, however, appears to be slightly more convex and exhibits a far greater irregularity in the arrangement, size, and shape of the individual cells.

Pl. bokkeveldense shows the closest affinity to *Pl. amazonicum* Katzer (Geologie des unteren Amazonasgebietes, p. 268, pl. ix, fig. 1 *a–d*, 1903), which is common in the Lower Devonian Conularia beds of Bolivia. (Kozlowski : " Faune Dévonienne de Bolivie," Annales de Paléontologie, 1923, vol. xii, p. 97, pl. x, fig. 1.) It differs, however, from this form by the very much greater number of its corallites and the far greater irregularity displayed in their dimensions, shape, and distribution.

It is interesting to note that all these closely allied forms occur in the Lower Devonian of such widely separated localities and that, moreover, their modes of occurrence and the rocks in which they occur are singularly alike.

Biological Notes.—It has already been mentioned that a radial symmetry such as that displayed by *Pl. lenticulare* is somewhat obscured in the case of *Pl. bokkeveldense*. It is interesting to note in this connection that also the perfect radial symmetry of the former type is only apparent and that in reality a bilateral symmetry forms the ground plan of these tabulate corals.* The outlines of the cells are forced on them by purely mechanical means and are conditioned by the space available. The mutual influence of the individual cells on further growth causes subsequent cells to become progressively more and more polygonal in outline, at first pentagonal and finally hexagonal.

In the case of *Pl. bokkeveldense* there is a prominent large cell situated very near the centre of the corallum. Its shape, however, while definitely polygonal, is irregular, and it is not followed by a regular cycle of more or less uniformly shaped cells. On the contrary, it is surrounded by a number of small and large cells in irregular, not strictly cyclic distribution. Succeeding this irregular cycle, a more regular and strongly marked cycle follows consisting of five large cells, not strictly uniform in size, separated by five considerably smaller cells of various sizes and stages of growth. That marginal part of the corallum, in which a sixth larger cell with its interstitial

* Beecher, Ch. E., " The Development of a Palaeozoic Poriferous Coral," Transac. Connecticut Acad. Arts and Sciences, vol. viii, 1891, p. 201 ; " Symmetrical Cell Development in the Favositidae," *ibid.*, p. 215.

small cell belonging to this cycle without a doubt was situated, is not preserved. Then follows a marginal cycle, most regular and distinct of all, of cells not as large as the inner cells, but showing a greater uniformity in size and outline. While the majority of the larger interior cells, though still recognisably polygonal, are almost rounded, even circular in outline, the cells of the marginal cycle have a pronounced polygonal outline, the latter varying with the amount of space available and the contours of the cells of the preceding cycle. It is to be noted that the outer contour of these marginal cells are almost invariably rounded (convex) and parallel to the almost circular outline of the whole corallum. The same feature is noticeable in the case of the preceding cycle of cells. Sharp angles generally only occur on sides facing the interior of the corallum.

Although the outer marginal cycle of cells appears so very much more regular, small, incipient interstitial cells on the very margin of the corallum may still be made out, thus showing that growth and enlargement were still actively going on when the colony of polyps perished, probably as a result of being detached from its foundation or buried by mud.

It is also to be noted that the interior cells, in accordance with the convexity of the surface of the corallum, are deepest and become progressively shallower towards the margin. This applies also to the smaller, *i.e.* younger, interstitial cells.

It is apparent from the above description that also in the case of the corallum of *Pleurodictyum bokkeveldense* growth evidently began from a central cell around which new cells gradually developed, and that in its primitive state its original ground plan, though not nearly as regular, resembled that of *Pl. lenticulare*. At an early stage of its growth at least six cells appear to have developed around the central cell, their different proportions being determined by the irregularity in outline of the central cell. Originally in juxtaposition and in close contact with themselves and the central cell, as growth went on they gradually began to diverge from the latter and one another like the sprouting stems of some varieties of grass. Their walls and that of the central cell appear to have been irregular in thickness. By nature already rather thick, more calcite was secreted by the various polyps in those parts where the divergence and interstice between neighbouring walls was greatest in order to effect a strengthening and prevent the disruption of the gradually growing corallum. Where the divergence and interstice between neighbouring walls became too great to be filled up by secretion and strengthening of opposite walls,

and where sufficient space became available, a new polyp took up its abode. The space thus set free within the corallum was utilised for the formation of a new cell, its outline being determined by the angles made by the adjoining walls and the angle of tapering of the new visceral cavity by the angle of divergence of the older cells from the central cell and one another, *i.e.* purely mechanically by the space available. Where this gradual divergence proceeded more slowly and the potential interstice could still conveniently be filled up by further secretion, *i.e.* a thickening of the adjoining and opposite walls, the formation of a new cell was correspondingly delayed. This process seems to have been continuous with the gradual addition of new cells, *i.e.* the growth of the whole corallum. Where the divergence of the older cells from one another and particularly from the central cell was sufficiently great, several new cells were formed in close proximity within the additional space thus available.

That there was a limit to this gradual enlargement of the corallum, and that it proceeded more or less uniformly around the whole of its margin and along certain definite lines, is shown by the fact that in each species of *Pleurodictyum* the same definite circular or oval outline is always maintained. As a matter of fact the whole compound corallum appears to behave like a single individual.

Reference must also be made to the fact that in the case of this specimen of *Pleurodictyum bokkeveldense* there is no trace of the worm-like appendage so frequently found within the centre of the corallum of other species of the genus *Pleurodictyum*. Although the nature of this appendage by some is still debated, there seems no doubt that it actually represents the cast of a worm either living as a parasite or in symbiosis with the coral, particularly in view of the fact that in Europe and America by no means all specimens exhibit this phenomenon. In addition, its frequency varies with the species found. Thus in North America it is most common in the Middle Devonian form *Pleurodictyum styloporum*, while in the other species it occurs with lesser and varying frequency. In Europe *Pleurodictyum problematicum* most frequently exhibits it. Further, since forms in various stages of growth, small and large, show the appendage to be of corresponding dimensions, it is certain that the worm grew with the coral. The fact that the worm has been overgrown by the corallum, and individual cells appear to have been affected by it both as regards outline and size, seems to indicate that it must have taken up its abode within the corallum at a fairly early stage of development of the latter.

Dacquè * favours the view that this curious phenomenon represents a case of symbiosis and that the worm was not a parasite. He argues that since the secretion of calcite is possible at any place within a coral exteriorly (theca) and interiorly (septa, dissepiments, and tabulae), the coral could easily have encased the worm by secreting calcite around it, analogous to the formation of a pearl within an oyster, if the worm had been an unwelcome intruder. Since, however, the coral made no attempt to do this, and the corallum, moreover, shows no sign of injury to its growth, he concludes that the worm lived in symbiosis with the coral and was not a parasite.

It is interesting to speculate whether any other specimens of the genus *Pleurodictyum* that may be found in the Bokkeveld beds in the future will exhibit this remarkable and interesting phenomenon.

* Dacquè, E., Vergleichende biologische Formenkunde der fossilen niederen Tiere, vol. ii, p. 473, Berlin, 1921.